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Research Article

Assessment of the vulnerability of Spiny Lizards in Central Mexico under anthropogenic pressure: integrating habitat suitability, landscape connectivity, fragmentation and protected area coverage

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Abstract

The genus *Sceloporus* represents a diverse and ecologically significant group of lizards within the Mexican herpetofauna, particularly in the Trans-Mexican Volcanic Belt (TMVB), a region of exceptional endemism increasingly threatened by anthropogenic pressures. In this study, we conducted a comprehensive spatial vulnerability assessment of 17 species of *Sceloporus* that are present in the TMVB, integrating ecological niche modelling (ENM), habitat fragmentation metrics, land-use exposure and protected area overlap. Binary distribution maps were generated from the ensemble models optimised with biomod2. For each species, we calculated the habitat area, number of habitat patches and mean patch size, synthesising these values into a composite vulnerability index. Land-use pressures were quantified through spatial overlaying of urban, agricultural and pasture-land layers, followed by principal component analysis (PCA) and k-means clustering to generate a multivariate anthropogenic pressure zonation. Species distributions were also compared against those of state and federal protected areas. The 17-species analysis revealed noteworthy variation in spatial dimensions and fragmentation of habitat, exhibiting high spatial vulnerability and high exposure to anthropogenic pressure. Furthermore, our results revealed that the predicted habitats of all 17 species overlap with highly transformed urban landscapes. A bivariate risk assessment identified *S. megalepidurus* as the only species with both high pressure and high vulnerability, while the species *S. anahuacus*, *S. albiventris* and *S. minor*, currently listed as "least concern" or "not evaluated" by the IUCN, showed alarming risk signals when spatially explicit metrics were incorporated. Our integrative framework underscores the need to revisit conservation assessments by incorporating habitat quality, fragmentation and exposure to land-use pressures, not just geographic range.

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Key words: Anthropogenic pressure, conservation prioritisation, ecological niche modelling, *Sceloporus* species, Trans-Mexican Volcanic Belt, vulnerability index

Introduction

Mexico ranks second worldwide in reptile diversity, with 1,031 documented reptile species, nearly half of which are endemic (Cabrera-Hernández et al. 2024; Uetz 2025). Despite this remarkable richness, many species face significant conservation challenges, including those classified as Data Deficient or Not Evaluated on the IUCN Red List – categories that inherently increase their vulnerability (Suazo-Ortuño et al. 2023). These risks are further compounded by factors such as restricted distribution ranges, dependence on specialised microhabitats and intensifying anthropogenic pressures (Rosas-Espinoza et al. 2024). Such threats are particularly pronounced in the Trans-Mexican Volcanic Belt (**TMVB**), a region where biodiversity and human activity intersect.

The TMVB spans Mexico from west to east and is widely recognised as one of the country's most ecologically complex and biogeographically significant regions (Smith 1941; Bryson et al. 2011; Gámez et al. 2012). Its diverse topography, pronounced climatic gradients and dynamic geological history have fostered exceptional levels of species richness and endemism, especially amongst amphibians and reptiles (Flores-Villela and Canseco-Márquez 2007; Sunny et al. 2017). Indeed, the TMVB ranks second in overall herpetological richness in Mexico and holds the highest number of endemic reptile and amphibian species (Flores-Villela and Canseco-Márquez 2007). Approximately a quarter of the nation's herpetofauna, more than 80% of which are endemic, are found within this biogeographic region (Lemos-Espinal and Smith 2024), underscoring its crucial role in the conservation of Mexico's vertebrate biodiversity. However, the ecological integrity of the TMVB is increasingly threatened by expanding urbanisation, agricultural intensification, deforestation and habitat fragmentation (Ochoa-Ochoa and Flores-Villela 2006; CONAPO 2010; Sunny et al. 2017; INEGI 2020). These pressures are exacerbated by the fact that the TMVB encompasses some of the most densely populated and industrially active regions in Mexico (González-Fernández et al. 2018). Although the establishment of protected natural areas (PNAs) has aimed to mitigate biodiversity loss, many of these areas are insufficiently managed or fail to represent key ecosystems and species (Ruiz-Reyes et al. 2024; Venegas-Barrera et al. 2024). As a result, large portions of biologically rich landscapes remain unprotected and are undergoing rapid environmental change (Sinervo et al. 2010; González-Fernández et al. 2022; Sunny et al. 2024a, 2024b). Sinervo et al. (2010) demonstrated that climate change has already driven substantial local extinctions in lizard populations, with 12% of Mexican populations disappearing since 1975. Their work validated physiological extinction risk models with empirical field data, projecting that, by 2080, local extinctions could reach 39% globally, with up to 20% of species lost. These alarming trends, confirmed across multiple continents, indicate that lizards have already crossed a threshold of climate-induced extinctions. When compounded with habitat degradation, fragmentation and loss of ecological connectivity, these climate-driven pressures threaten to accelerate biodiversity loss, particularly in ecologically sensitive and poorly-protected

regions, such as the Trans-Mexican Volcanic Belt (Mastretta Yanes et al. 2015; González-Fernández et al. 2018; Sunny et al. 2022; Rubio-Blanco et al. 2024). Understanding how species respond to these pressures is essential for effective conservation planning (Tischendorf and Fahrig 2000; Bennett 2003; Guisan and Thuiller 2005; Guisan et al. 2013; Maciel-Mata et al. 2015; Ersoy et al. 2018). This is particularly important for taxa, such as the genus *Sceloporus*, which is emblematic of Mexican herpetofauna. With approximately 110 recognised species – 106 of which are endemic to Mexico (Wiens et al. 2010; Uetz 2025) – *Sceloporus* represents a highly diverse lineage of spiny lizards that occupy a wide range of habitats, including montane forests, arid scrublands and grasslands. Despite the ecological importance and diversity of this group, there are significant knowledge gaps regarding the environmental factors that influence their distribution, as well as their vulnerability to anthropogenic pressures (Smith 1941; Sites et al. 1992; Wiens and Reeder 1997; Smith and Ballinger 2001; Flores-Villela and Canseco-Márquez 2004; Leaché 2010; Leaché et al. 2016; Martínez-Méndez et al. 2019).

Moreover, although efforts have been made to characterise the thermal physiology, systematics and biogeographic history of *Sceloporus* species, fewer studies have integrated ecological niche modelling with multivariate pressure mapping, landscape fragmentation analysis and protected area overlap assessments (Leaché et al. 2010, 2016; López-Reyes et al. 2024; García-Rosales et al. 2024). These integrative approaches are necessary to evaluate whether current conservation instruments adequately protect the most vulnerable species and to identify areas where conservation gaps persist. The TMVB, with its high levels of endemism and strong anthropogenic pressure, is an ideal natural laboratory for implementing these tools and advancing conservation science.

Despite their broad distribution, most *Sceloporus* species included in this study are currently classified as “Least Concern” (LC) by the IUCN Red List or have not been evaluated. Amongst them, *S. megalepidurus* is listed as Vulnerable (VU), while *S. anahuacus*, *S. bicanthalis*, *S. bulleri*, *S. dugesii*, *S. grammicus*, *S. horridus*, *S. mucronatus*, *S. palaciosi*, *S. scalaris* and *S. torquatus* are considered LC. In contrast, *S. subniger*, *S. albiventris*, *S. melanogaster*, *S. minor*, *S. utiformis* and *S. variabilis* have not yet been assessed (IUCN 2025). According to the Mexican official normative (NOM-059-SEMARNAT 2025), only *S. grammicus* and *S. megalepidurus* are listed as species under special protection (SEMARNAT 2025). This disparity underscores a critical limitation of global conservation assessments, which often rely on broad-scale distribution data and may underestimate species’ actual vulnerability to localised anthropogenic pressures.

Addressing these gaps requires regional, fine-scale evaluations that integrate multiple indicators, such as ecological niche modelling, habitat fragmentation, land-use exposure and representation within protected areas. In this context, our study assessed the vulnerability of 17 *Sceloporus* species occurring in the Trans-Mexican Volcanic Belt (TMVB), providing updated insights into their conservation status. Our main objectives were to: (1) model the potential distribution of each species using ecological niche modelling techniques, including both Maxent via the ENMeval package and an ensemble approach integrating eight algorithms implemented in biomod2; (2) quantify the degree of habitat fragmentation and patch isolation using landscape metrics; (3) assess the overlap between species distributions

and anthropogenic land-use pressures, including urban areas, agriculture and cultivated pastures; and (4) evaluate the degree to which each species is represented within federal and state protected areas. We hypothesised that species with smaller and more fragmented distributions would be more exposed to anthropogenic land use and have lower protection coverage, thereby facing a compounded risk of extinction.

Materials and methods

The Trans-Mexican Volcanic Belt (TMVB) is a Neogene volcanic arc covering approximately 160,000 km^2 across central Mexico that extends from 18°30'N to 21°30'N (Ferrari et al. 2018). Formed by the subduction of the Cocos and Rivera plates beneath the North American Plate, the TMVB is characterised by a chain of stratovolcanoes, volcanic fields and extensive highlands (Gómez-Tuena et al. 2005; Ferrari et al. 2012). Its rugged topography reaches elevations exceeding 4,000 m above sea level (m a.s.l.). The region's complex geological history – marked by multiple volcanic episodes, tectonic activity and climatic fluctuations – has shaped a mosaic of habitats ranging from temperate forests and alpine grasslands to xerophytic scrublands (Mastretta-Yanes et al. 2015). These environmental gradients have fostered exceptional levels of species richness and endemism, making the TMVB a key biogeographic corridor and a biodiversity hotspot of global significance (Flores-Villela and Canseco-Márquez 2007; Morrone 2014). Despite its importance, several aspects of its geological evolution, ecological connectivity and response to anthropogenic pressures remain poorly understood. To investigate patterns of habitat suitability and conservation within this region, we compiled occurrence data for 17 lizard species of the genus *Sceloporus*, each with distributions overlapping portions of the TMVB (Arriaga et al. 1997). Species selection followed the criteria proposed by Campillo-García et al. (2021), particularly regarding taxonomic updates within the *S. torquatus* complex. Occurrence records were sourced from the iNaturalist online repository (https://www.inaturalist.org/) and consolidated from multiple biodiversity databases, including REMIB, UNIBIO, GBIF, HERPNET, VertNet and IREKANI, ensuring a comprehensive and updated dataset. To ensure data currency, only records from 2000 to 2023 were considered. To ensure model accuracy and mitigate potential sampling biases that might induce model overfitting (Boria et al. 2014), the obtained data were filtered using the NicheToolBox online tool (Osorio-Olvera et al. 2020). Duplicate observations within the same pixel, approximately 1 km^2 in resolution, were eliminated, employing a δ threshold value of 0.0083333. Furthermore, records lacking precise coordinates, sampling year information or data falling beyond Mexican territorial confines were systematically excluded. After filtering, the dataset included, 61 for *S. albiventris*, 34 for *S. anahuacus*, 44 for *S. bicanthalis*, 17 for *S. bulleri*, 63 for *S. dugesii*, 621 for *S. grammicus*, 238 for *S. horridus*, 40 for *S. megalepidurus*, 132 for *S. melanogaster*, 235 for *S. minor*, 140 for *S. mucronatus*, 22 for *S. palaciosi*, 97 for *S. scalaris*, 122 for *S. subniger*, 255 for *S. torquatus*, 111 for *S. utiformis* and 440 for *S. variabilis* (See Suppl. material 1: table S1). The dataset is publicly available at: Zenodo. https://doi.org/10.5281/zenodo.16879333.

Environmental variables

Three categories of environmental variables were employed to construct the ecological niche models: land use and vegetation, topographic and climatic. Land-use and vegetation data were sourced from the National Institute of Statistics and Geography for the year 2016 (INEGI 2016), while topographic data were obtained from a digital elevation model at a scale of 1:50000 (INEGI 2016). Climate data encompassing 19 climatic and 12 solar radiation variables were sourced from WorldClim (Hijmans et al. 2005), with a spatial resolution of 30 arc-seconds (approximately 1 km^2). The land-use map underwent reclassification to delineate different classes, which were subsequently transformed into continuous variables using the filter module of IDRISI SELVA 17.0 (Clark Labs 2012). All layers were processed in raster format with a resolution of 1 km^2 utilising the raster (Hijmans and Van Etten 2016) and rgdal (Bivand et al. 2015) packages in R software (version 4.4.2; R. Development Core Team 2024). Furthermore, Pearson's correlation analysis was conducted to identify and eliminate highly correlated variables ($r^2 > 0.7$; Dormann et al. (2013)), facilitated by the ENMtools and usdm packages in EcoNicheS (Sunny et al. 2025) for R software. The resulting layers were utilised in the preparation of ecological niche models (ENMs; See Suppl. material 1: table S2).

Accessibility areas

We generated the accessibility area (*M*) for each species using ArcMap software and the R programming language (ESRI 2020; R Studio Team 2021). We used delimitation to follow the biogeographic region containing the records of each species in Mexico (Arriaga et al. 1997; Sunny et al. 2017, 2024a, 2024b; González-Fernández et al. 2018; Rubio-Blanco et al. 2024) (Fig. 1, See Suppl. material 1: fig. S1).

Ecological niche modelling

To ensure a robust and comparative framework for ecological niche modelling, we employed two complementary approaches: Maxent modelling through the ENMeval package and ensemble modelling using the biomod2 package. The use of Maxent via ENMeval allowed us to explore the influence of different parameter settings (feature classes and regularisation multipliers) on model performance and spatial predictions, providing a detailed understanding of how algorithm configuration can affect outcomes. Simultaneously, we implemented ensemble models in biomod2, integrating eight commonly used algorithms (including Maxent) to generate consensus predictions that are generally more stable and less sensitive to the assumptions of individual methods. By comparing the results obtained from these two modelling strategies, we aimed to assess the consistency of spatial patterns across different methodological frameworks. This dual approach not only strengthens the reliability of our findings, but also highlights potential areas of uncertainty, which is critical when providing information for conservation strategies, based on species distribution models.

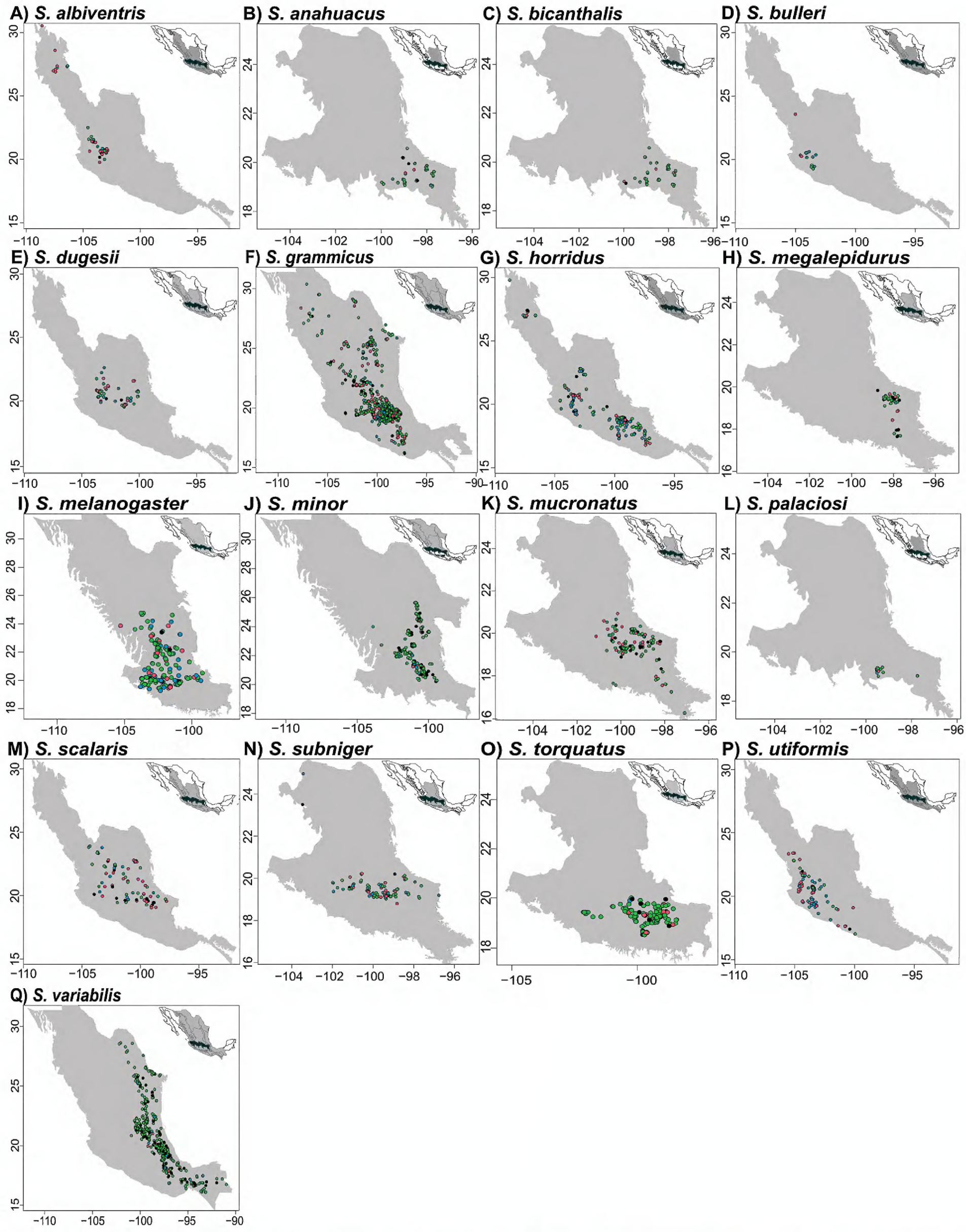

Figure 1. Accessibility areas (M) for each species (dark grey polygons) and occurrence records used in ecological niche models for 17 species of *Sceloporus*. Coloured dots represent occurrence data, with colours corresponding to the spatial partitions used for model calibration and evaluation. For most species, the block partitioning method was applied; however, for *S. bulleri* and *S. palaciosi*, a jackknife partitioning method was used due to the low number of records. In the upper right corner, a map of Mexico (in grey) shows the study area M for each species, with the Trans-Mexican Volcanic Belt (TMVB) highlighted in green.

ENMeval: Maximum entropy algorithm

The maximum entropy algorithm was implemented using Maxent 3.3.3 software (Phillips et al. 2006) in conjunction with species-specific optimisations facilitated by the ENMeval package (Muscarella et al. 2014) in R software (R Studio Team 2021). The construction of species-specific ecological niche models was based on occurrence records and preselected environmental variables. To ascertain the optimal model settings, a preliminary test was conducted using the ENMeval package, encompassing all feasible combinations of parameters. This pilot test selected regularisation values of 1 and 2, along with characteristic classes, including "linear" (L), "quadratic" (Q), "product" (P), "threshold" (T) and "hinge" (H), encompassing combinations, such as L, H, LQ, LQP, LQH, LQHP and LQHPT. Additionally, 100,000 random points were generated as background points during the modelling process by utilising partitioning methods, namely, "Block", "Checkerboard 1" and "Checkerboard 2". For species with limited records, such as *S. bulleri* and *S. palaciosi*, the "jackknife" data partitioning method was employed. Optimal parameter combinations for each species were determined, based on the corrected Akaike Information Criterion (AICc) (Warren et al. 2010; Warren and Seifert 2011). Model accuracy and reliability were assessed using various approaches, including the area under the curve (AUC) and transformation of the AUC into a partial receiver operating characteristic (ROC) curve, facilitated by the ntbox package in R software.

biomod2

An ensemble model was also constructed with the biomod2 package (Thuiller et al. 2025) implemented in the shinydashboard package EcoNicheS for R. Eight of the ten algorithms available in the package were selected. These models included the generalised linear model (GLM), generalised boosting model (GBM), generalised additive model (CTA), artificial neural network (ANN), surface range envelope or BIOCLIM (SRE), flexible discriminant analysis (FDA), random forest (RF), Maxent and MaxNet. As presence data were available, a set of 100000 pseudoabsence data points was randomly generated in EcoNicheS for R. The prevalence was set to 0.5 to ensure the presence or absence of the same importance in the calibration process (Barbet Massin et al. 2012; Linero et al. 2020). The models were calculated ten times, each run with a different selection of training and testing datasets. The proportion of data for calibration was set to 70% (Linero et al. 2020).

To evaluate the overall model accuracy of both the Maxent and ensemble models, the area under the curve (AUC) from the receiver operating characteristic (ROC) plot was used first (Metz 1978; Phillips et al. 2006), followed by the transformation of the area under the curve (AUC) into a partial receiver operating characteristic (PROC) curve (partial ROC; Peterson et al. (2008)). For this purpose, the package EcoNicheS (Sunny et al. 2025) in R was used. For the ensemble model, the true skill statistic (TSS) was calculated with the package biomod2 (Allouche et al. 2006), based on the sum of sensitivity and specificity minus one (the sensitivity is the proportion of correctly predicted presences and the specificity is the proportion of correctly predicted absences). In the biomod2 approach, the models were assembled by a total consensus rule and algorithms were assembled by the weighted sum of evaluations greater than TSS > 0.8 (Linero et al. 2020; Var-

gas-Jaimes et al. 2021). The ensemble model (seven algorithms × 10 repetitions) was subsequently used to project the potential distributions of the species. To evaluate the potential distribution areas of Spiny Lizards, we applied two threshold criteria: the presence of training in the 10th percentile and the presence of training in the 80th percentile. The 10th percentile represents a more permissive threshold, often used to capture the full potential range of a species, including marginal habitats. In contrast, the 80th percentile is a more conservative and ecologically realistic threshold and is especially suitable for assessing vulnerability in the species studied. These analyses were performed using the EcoNicheS package in R.

Landscape connectivity

Functional connectivity analysis was performed with a circuit theory (CT) model, utilising a landscape scenario as a resistance surface (Mateo-Sánchez et al. 2014) implemented through Circuitscape v. 4.0 software (McRae et al. 2013). The resistance surface layers were derived from habitat suitability maps generated with the ENMeval package and computed using the inverse transformation equation (1 − MNE), where MNE represents the ecological niche model output. Given the constraints in modifying processor numbers within the Circuitscape v. 4.0 interface, Julia 1.8.2 (Bezanson et al. 2017) software was used to calculate habitat connectivity for species with abundant presence records. The resulting maps were visualised and exported in ArcMap. Furthermore, the identification of specific connectivity areas (corridors, linkages, stepping stones) in geographic space involved analysing the overlap between the Protected Natural Areas polygons and species-specific connectivity models.

Habitat fragmentation analysis (number of patches)

To quantify habitat fragmentation for each species, *Sceloporus*, we used threshold binary distribution maps with a presence value ≥ 80 (on a 0–100 suitability scale). Raster maps were processed using the terra package (Hijmans 2025) in R. Each binary map was first converted into a clump map, which assigns unique IDs to contiguous patches (clumps) of presence cells. The number of patches per species was then calculated using the clump output, excluding the NA values. This approach allowed us to estimate both the total number of habitat patches (a proxy for fragmentation) and the mean patch size by dividing the total area by the number of patches. All raster analyses were conducted at a consistent resolution and coordinate reference system across the study area.

Anthropogenic pressure index and habitat exposure

To quantify species exposure to anthropogenic pressures, we overlaid each species' binary habitat suitability map with three rasterised land-use layers representing major human activities: urban areas (U), agriculture (A) and cultivated pastures (P). A threshold was applied for all habitat suitability maps using a value of ≥ 80 (on a 0–100 scale), producing binary maps of suitable habitat. These binary maps and land-use layers were processed in R using the terra package. Each anthropogenic pressure layer was coded as 1 (presence of pressure) or 0 (absence) and combined with the species' distribution raster.

For each pixel within a species' distribution, we calculated an Anthropogenic Pressure Index (API) using the following equation:

$$API = U + A + P$$

where:
U = 1 if the pixel overlaps with urban areas, 0 otherwise;
A = 1 if the pixel overlaps with agricultural land, 0 otherwise;
P = 1 if the pixel overlaps with cultivated pastures, 0 otherwise.

This pixel-level index ranges from 0 (no anthropogenic pressure) to 3 (overlap with all three pressures), representing the cumulative number of anthropogenic pressures affecting each cell. To summarie the overall impact, we calculated the percentage of suitable habitat under anthropogenic pressure for each species using the following formula:

$$\textit{Pressure Index}(\%) = (\textit{Total suitable habitat cells}) \times 100$$

This index reflects the proportion of each species' predicted habitat affected by at least one anthropogenic pressure. The results were visualised using horizontal bar plots with a continuous colour gradient (blue to red) to represent increasing levels of pressure, created using the ggplot2 package. This index was a key component of our integrative vulnerability assessment, helping to identify species whose ranges are disproportionately exposed to human land-use conversion across TMVB.

Multivariate pressure zonation (PCA and k-means)

To spatially delineate regions of cumulative anthropogenic pressure, we performed a principal component analysis (PCA) on the binary urban, agricultural and pasture layers using the RStoolbox (Müller et al. 2024) and stats (R Core Team 2024) packages. The first three principal components were extracted to represent key gradients in human land use. These components were then clustered using the kmeans function from base R (stats package) with k = 4 to define multivariate pressure zones across the TMVB. Each zone was assigned to one of four pressure classes: low pressure: natural or semi-natural areas. Moderate pressure: Low-intensity agriculture or pastures. High pressure: Mixed agricultural–urban mosaics. Very high pressure: Urban or industrialised areas. This zonation was used to calculate the distribution of each species across pressure categories.

Composite vulnerability and pressure integration

To assess overall extinction risk, we integrated two key metrics: the spatial vulnerability index (based on habitat fragmentation and isolation) and the total anthropogenic pressure index (based on the overlap with land-use threats). Both indices were plotted in a bivariate space to classify each species into one of four risk categories: High risk – high vulnerability and high exposure; Pressure-only – high exposure, but low spatial vulnerability; Vulnerability-only – high spatial fragmentation, but low exposure to anthropogenic pressure; and Low risk – low values for both indices. This classification was visualised using

a scatterplot with quadrant divisions generated in R, using the ggplot2 package (Wickham 2016). This integrative framework enabled the identification of species exhibiting mismatches between ecological risk and current conservation status, highlighting priorities for re-assessment and protection.

Forest loss trend analysis (2001–2023)

To evaluate historical forest cover loss across the Trans-Mexican Volcanic Belt (TMVB), we used tree cover loss data from the Global Forest Watch platform (https://www.globalforestwatch.org/; Hansen et al. 2013). The dataset represents annual tree cover loss (in thousands of hectares) from 2001 to 2023. As raw raster downloads were unavailable due to GFW server restrictions, numerical values were manually extracted from the interactive bar graph. These values were converted from thousands of hectares (kha) to square kilometres (km^2) by multiplying each value by 10. The resulting time series was plotted in R using the ggplot2 package to produce a bar chart illustrating annual forest loss (km^2). The total forest loss over the 23-year period was also calculated and temporal patterns were analysed. The dataset included areas with a canopy loss greater than 30% for vegetation taller than 5 metres. To assess long-term trends, we applied linear regression analysis using the base R lm() function, modelling annual forest loss (dependent variable) as a function of year (independent variable), following established methods for trend detection in ecological time series (Zuur et al. 2009). The statistical significance of the trend was evaluated using a Pearson correlation test (Sokal 1995). Finally, we visualised the results in ggplot2 by adding a fitted linear regression line with 95% confidence intervals.

Results

Ecological niche modelling

We derived potential distribution maps for 17 spiny lizard species using two modelling methods: Maxent in ENMeval and ensemble model in biomod2. The evaluation of the performance of Maxent with the ENMeval and area under the curve (AUC) analyses confirmed that the Maxent models performed significantly better than expected (*AUC* = 0.901–0.997; *p* < 0.001). The partial ROC test further supported the model robustness, with an empirical *AUC* ratios ≥ 1.799–1.985 (*p* < 0.001 in all cases; Table 2). We selected the optimal model for each species, based on the lowest AICc values (Table 1). In Fig. 2, a visualisation of the ENMeval potential distribution models for each species, while the response curves of the various environmental variables are detailed in Suppl. material 1: tables S3–S19.

Species potential distribution

S. albiventris occurred primarily across the TMVB, Pacific Coast (CP), Sierra Madre Occidental (SMOc) and a small segment of the AS (Fig. 2A). The minimum temperature of the coldest month (BIO6; 21.9% contribution) most strongly influenced its distribution, with an optimal range of 5–10 °C. The urban areas (11.6% contribution) were positively correlated with their presence,

Table 1. Best models in ENMeval considering the combination of feature classes and the regularisation multiplier for each *Sceloporus* species.

ENMeval					
Species	**Feature classes (fc)**	**Regularisation multiplayer (rm)**	**Partial-ROC**	**AUC**	**AICc**
S. albiventris	LQ	2	1.915	0.985	877.50
S. anahuacus	LQ	2	1.965	0.988	490.55
S. bicanthalis	L	1	1.972	0.949	15551.21
S. bulleri	L	2	1.912	0.955	436.23
S. dugesii	LQ	1	1.905	0.935	5857.28
S. grammicus	LQHPT	1	1.92	0.943	2446.36
S. horridus	LQHPT	2	1.87	0.960	27485.16
S. megalepidurus	LQHP	1	1.985	0.967	3153.55
S. melanogaster	LQ	1	1.844	0.980	2839.63
S. minor	LQ	1	1.887	0.951	1581.70
S. mucronatus	LQ	2	1.886	0.901	2391.16
S. palaciosi	L	2	1.976	0.941	3202.14
S. scalaris	LQ	2	1.799	0.943	5749.33
S. subniger	LQHP	1	1.96	0.984	689.32
S. torquatus	LQ	2	1.941	0.941	500.2
S. utiformis	LQ	1	1.881	0.919	4212.28
S. variabilis	LQHPT	1	1.897	0.997	394.93

as was their elevation (11.3%; optimal range: 600–1200 m). *S. anahuacus* exhibited a distribution largely restricted to the TMVB mountainous regions (Fig. 2B). Three variables primarily determined its occurrence: *Abies* forest coverage (25.8%; positive effect), elevation (25.3%; positive influence) and December solar radiation (Srad12; 25.2%), with the probability of occurrence increasing markedly above 14,500 kJ/m^2/day. *S. bicanthalis* was mainly distributed in the TMVB, with minor extensions into the SMOr and AS (Fig. 2C). The key contributing variables included BIO5 (24.5%; negative effect above 19 °C), *Pinus* forest coverage (24.1% negative effect) and high mountain grassland (18% negative effect). *S. bulleri* exhibited a broad distribution across western Mexico, spanning the TMVB, CP, SMOc and AS regions (Fig. 2D). March solar radiation (Srad3; 60.8% contribution) was the dominant variable, with the presence probability increasing above 20,500 kJ/m^2/day. Precipitation in the wettest month (BIO13; 13.9%) and in the arid vegetation season (9.5%; negative effect) were also important. *S. dugesii* occurred in central Mexico, including in the TMVB, AS, SMOc and CP regions (Fig. 2E). March solar radiation (Srad3; 43.3%) exhibited the strongest positive association, particularly above 20,500 kJ/m^2/day. Additionally, the probability of their presence being above 50% is related to the temperature range of 4–7 °C BIO6 (contribution of 26.5%). *S. grammicus* exhibited one of the most extensive distributions, covering the TMVB, SMOr, AS, AN, PT, PO and SMS regions (Fig. 2F). Urban areas (30.7%) exhibited the strongest positive association, followed by elevation (25.8%; positive). However, the maximum temperature (BIO5; 22.4%) was negatively correlated with BMI, indicating an increased probability of infection below 24 °C.

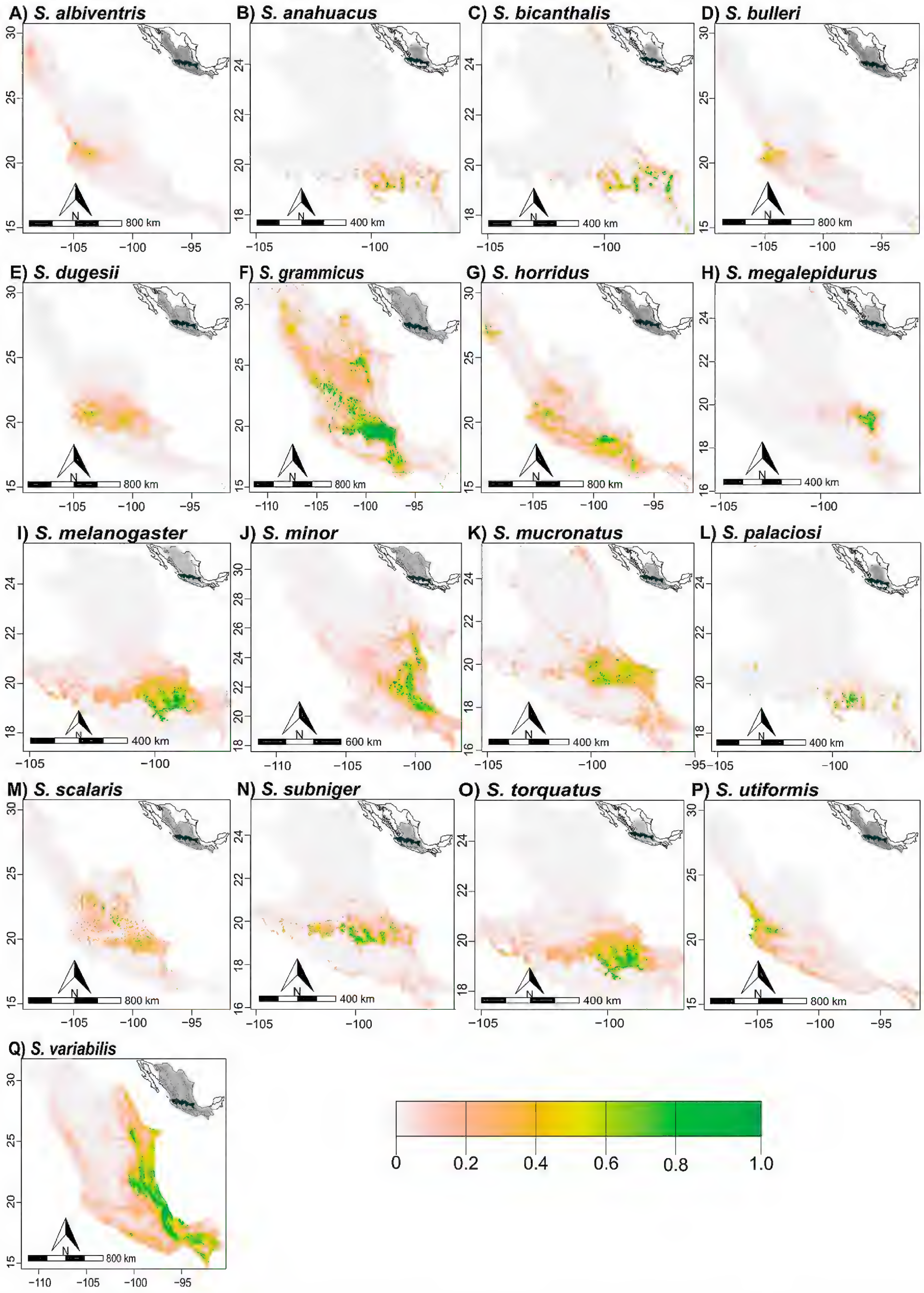

Figure 2. Potential distributions of 17 species of Spiny Lizards of the genus *Sceloporus* using the Maxent algorithm with the ENMeval package in R. In the upper right corner, a map of Mexico (in grey) shows the study area M for each species, with the Trans-Mexican Volcanic Belt (TMVB) highlighted in green.

Table 2. Evaluation values of ecological niche models with biomod2.

	biomod2			
Species	**Partial-ROC**	**Kappa**	**TSS**	**ROC**
S. albiventris	1.989	0.921	0.993	0.999
S. anahuacus	1.995	0.911	0.993	0.999
S. bicanthalis	1.981	0.912	0.92	0.994
S. binocularis	1.999	0.938	0.991	0.999
S. bulleri	1.98	0.971	0.999	1
S. dugesii	1.978	0.922	0.957	0.997
S. grammicus	1.947	0.928	0.961	0.997
S. horridus	1.955	0.911	0.909	0.994
S. megalepidurus	1.972	0.932	0.968	0.998
S. melanogaster	1.978	0.902	0.978	0.997
S. minor	1.97	0.929	0.991	0.999
S. mucronatus	1.949	0.897	0.971	0.998
S. palaciosi	1.99	0.915	0.956	0.996
S. scalaris	1.941	0.946	0.963	0.998
S. subniger	1.972	0.923	0.99	0.999
S. torquatus	1.951	0.880	0.992	0.992
S. utiformis	1.957	0.858	0.864	0.985
S. variabilis	1.936	0.941	0.998	1

S. horridus ranged widely across the Balsas Depression, SMS, TMVB, CP, SMOc, PO and part of the AS (Fig. 2G). Urban area (25%; positive), *Pinus* forest coverage (19.1%; negative) and BIO5 (18%; positive) were the primary determinants. *S. megalepidurus* showed a restricted distribution in the TMVB and SMS, with minor occurrences in the SMOr and AS (Fig. 2H). BIO6 (37.9%; negative with increasing temperature), June solar radiation (Srad6; 25.6%; negative) and BIO13 (10.7%; negative) were the main contributors.

ASs in *S. melanogaster* spread widely from the TMVB to the SMOc (Fig. 2I). December and June solar radiation (Srad12: 13.8%; Srad6: 12%) exhibited optimal ranges of 13,000–19,500 kJ/m^2/day. BIO6 (37.9%) had a minimum tolerable temperature ranging from 3–9 °C, while arid vegetation (11.9%) had negative effects. In addition, agricultural cover (11.7%) favoured their presence at ~ 60% coverage.

S. minor was primarily distributed in northern Mexico (AS, SMOr, AN and part of the TMVB; Fig. 2J). The key variables included March solar radiation (24.1%; positive), minimum precipitation (23.9%; low tolerance above 100 mm) and maximum temperature (18.5%; optimal range: 15–29 °C).

S. mucronatus ranges across the TMVB, SMOr, AS, SMS and part of the PO (Fig. 2K). The maximum temperature (42.6%) exhibited a negative correlation, with a more regular correlation occurring at 13 °C, which decreased to 50% at 24 °C. December solar radiation (12.4%; positive) and intermediate urban area coverage were also influential. *S. palaciosi* was confined to the TMVB (Fig. 2L), the distribution of which was primarily determined by December solar radiation (29.1%; positive), urban areas (26.8%; positive) and maximum temperature (BIO5; probability decreased above 13 °C). *S. scalaris* exhibited the widest distribution (AS, TMVB, SMS, SMOc and SMOr; Fig. 2M). Elevation (39.3%) was

most important, with a 50% occurrence probability above 2,500 m increasing to 90% at 4,000 m. The minimum temperature (20.9%) defined a tolerance range of 0–5 °C. *S. subniger* predominantly occupied the Trans-Mexican Volcanic Belt (TMVB), Sierra Madre Oriental (SMOr) and a small portion of the Southern Altiplano (AS) (Fig. 2N). The maximum temperature of the warmest month (BIO5) was the most influential variable (35.9% contribution), showing a 60% presence probability at 22 °C that increased with cooler temperatures. Arid vegetation coverage (14.2%) was negatively correlated with forest presence, while *Abies* forest coverage (13.4%) was positively correlated with forest presence. *S. torquatus* occurred primarily within the TMVB, with minor extension into the AS (Fig. 2O). December solar radiation (35.3%), urban area (19.6%) and maximum temperature (13.1%; optimal range: 13–26 °C) were key variables. *S. utiformis* ranged along western Mexico (CP, TMVB, Balsas Depression, part of the AS; Fig. 2P). March solar radiation (30.8%) was most influential, followed by elevation (17.1%; preference for 0–800 m) and arid vegetation (10.7%; negative effect). *S. variabilis* had the broadest distribution (AS, Gulf of Mexico; SMOr, PO, Chiapas Heights; Soconusco, PT; and parts of the TMVB/CP; Fig. 2Q). March solar radiation, minimum temperature and urban area were the primary associated variables. All the models demonstrated strong performance (ROC-partial: 1.257-1.999; Kappa: 0.858-0.971; TSS: 0.864-0.999; ROC: 0.985-1; Table 2).

According to the potential distribution maps generated through this model, species such as *S. anahuacus*, *S. bicanthalis*, *S. dugesii*, *S. grammicus*, *S. megalepidurus*, *S. melanogaster*, *S. mucronatus*, *S. palaciosi*, *S. subniger* and *S. torquatus* exhibited the highest habitat suitability values within the TMVB biogeographic region (Fig. 3B, C, E, F, H, I, K, L, N, O). When comparing potential distribution areas in square kilometres (km^2) obtained from the two methods employed for the construction of the ecological niche models (ENMs), it became evident that the optimised ensemble model algorithm produced larger potential distributions than did the Maxent optimised in ENMeval. Notably, *S. variabilis* consistently exhibited the largest suitable area, while *S. anahuacus* exhibited the narrowest suitable area (Table 3). The spatial patterns observed in the potential distribution maps generated using the ENMeval algorithm were broadly consistent with those produced by biomod2 (Fig. 3). However, in all the cases, biomod2 yielded slightly larger predicted distribution areas than did ENMeval (Table 3).

The landscape connectivity analysis revealed significant variation in the species (Fig. 4). Species with restricted distributions in the Trans-Mexican Volcanic Belt (TMVB) mountains (*S. anahuacus*, *S. bicanthalis*, *S. bulleri*, *S. megalepidurus* and *S. palaciosi*; Fig. 4) exhibited particularly low connectivity, with minimal or no linkages between suitable habitat patches, indicating high fragmentation. In contrast, widespread species (*S. grammicus* and *S. variabilis*) had the highest connectivity values (Fig. 4F, Q). The TMVB emerged as a critical connectivity hub, serving as the primary habitat for 14 of the 17 studied species (excluding *S. minor*, *S. torquatus* and *S. variabilis*). The TMVB network is divided into two connectivity areas, bifurcating into the eastern and western regions. In the Eastern region, pivotal connectivity areas included the Sierra de las Cruces, Nevado de Toluca, Iztaccíhuatl-Popocatépetl and the Monarch Butterfly Biosphere Reserve, fostering significant connectivity across multiple species. Additionally, a potential corridor was identified south of the Toluca Valley, notably influencing species, such as *S. subniger*, *S. anahuacus*, *S. bicanthalis* and *S. mucronatus*. In the Western region,

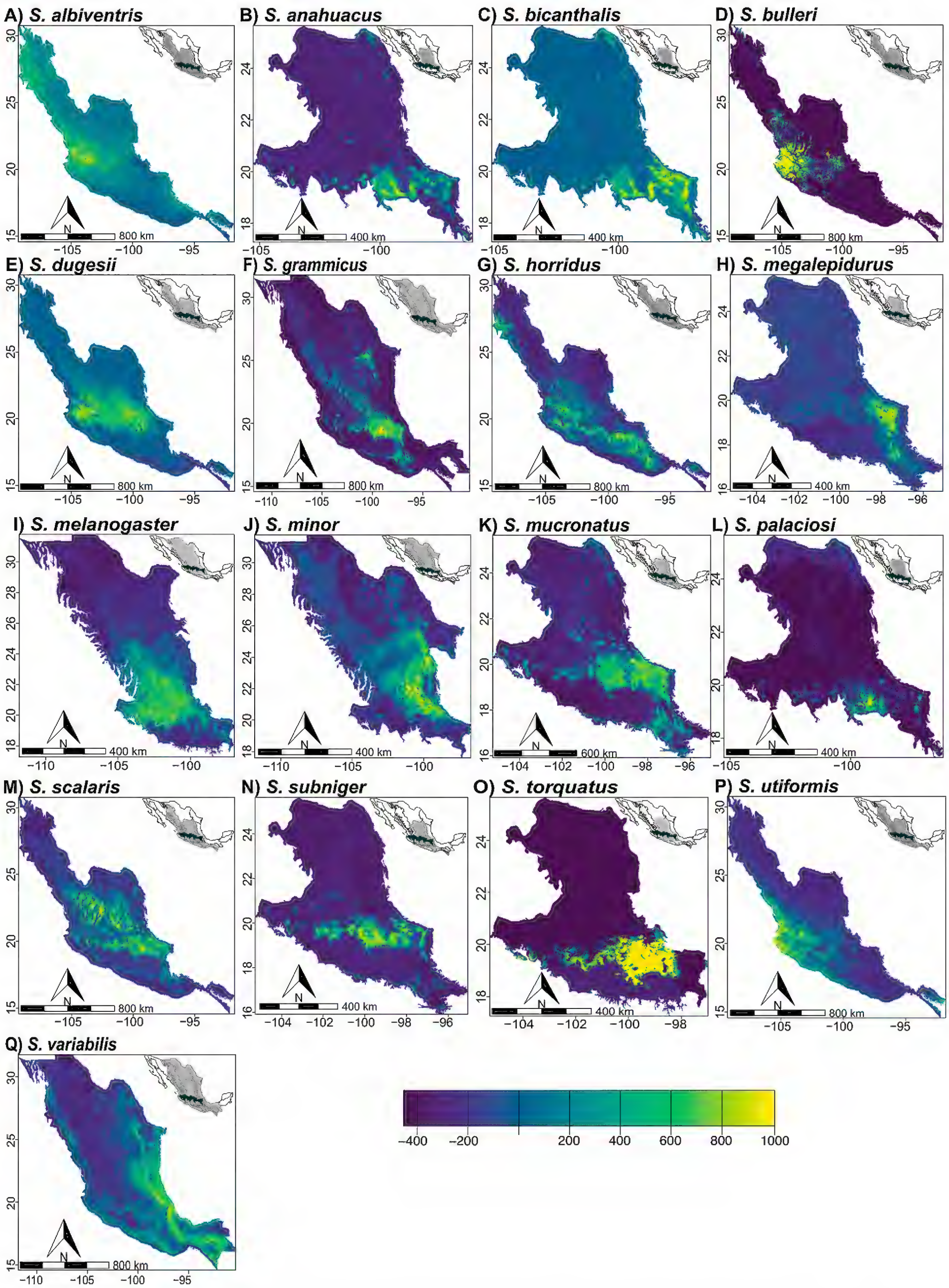

Figure 3. Potential distributions of the 17 species of Spiny Lizards in the genus *Sceloporus* using the ensemble model with the biomod2 package in R. In the upper right corner, a map of Mexico (in grey) shows the study area M for each species, with the Trans-Mexican Volcanic Belt (TMVB) highlighted in green.

Table 3. Potential distribution area of lizards of the genus *Sceloporus* in the Mexican territory calculated in km^2 for the two algorithms used, using the 10th percentile value.

Species	10th percentile value	ENMeval	biomod2
		km^2	km^2
S. albiventris	0.166	112,705.6	187,709.32
S. anahuacus	0.167	11,994.5	57,995.51
S. bicanthalis	0.176	14,938	51,896.62
S. bulleri	0.384	97,380.2	82,466.86
S. dugesii	0.309	93,919.8	154,462.6
S. grammicus	0.211	162,105	280,138.91
S. horridus	0.239	163,002.2	217,905.88
S. megalepidurus	0.272	12,374.1	24,725.56
S. melanogaster	0.261	179,567	380,387.21
S. minor	0.235	127,956.5	270,620.19
S. mucronatus	0.175	73,933.7	457,427.91
S. palaciosi	0.289	14,326.2	14,359.08
S. scalaris	0.169	251,970.4	400,727.4
S. subniger	0.155	34,206.1	89,236.87
S. torquatus	0.189	28,902.4	52,763.1
S. utiformis	0.277	113,330.9	148,089.93
S. variabilis	0.198	267,366.8	150,5482.92

the connectivity values are concentrated in the Jalisco Valley area and the central part of Nayarit State. Notably, a corridor spanning between these regions, particularly evident in the Municipality of Ixtlán del Río in Nayarit, facilitated connectivity for species such as *S. albiventris*, *S. bulleri*, *S. horridus* and *S. utiformis*.

Habitat fragmentation, spatial vulnerability and composite vulnerability indices

Binary distribution maps (threshold ≥ 80) revealed substantial variation in habitat size and fragmentation across species (Fig. 5). The number of habitat patches ranged from a single patch (e.g. *S. scalaris*) to more than 500 (e.g. *S. minor*) (Fig. 5A), indicating substantial heterogeneity in landscape continuity. Species with fewer and larger patches (e.g. *S. melanogaster*, *S. mucronatus*, *S. scalaris* and *S. variabilis*) exhibited lower fragmentation (Fig. 5A, B), while those with many small patches (e.g. *S. minor*, *S. albiventris* and *S. anahuacus*) were considered more fragmented (Fig. 5A, B). Five species (*S. minor*, *S. albiventris*, *S. anahuacus*, *S. subniger* and *S. bulleri*) exhibited the greatest vulnerability.

The composite vulnerability index (Fig. 5C) integrates habitat area, number of habitat patches and average patch size. This finding revealed substantial variation amongst the *Sceloporus* species. *Sceloporus minor* exhibited the highest vulnerability score, indicating a combination of small, fragmented and isolated habitat patches. Furthermore, *S. anahuacus*, *S. albiventris* and *S. megalepidurus* also exhibited high vulnerability values, suggesting a concerning spatial configuration of their potential habitats that may restrict population viability and dispersal. Mid-vulnerability level scores were calculated for *S. subniger*, *S. palaciosi* and

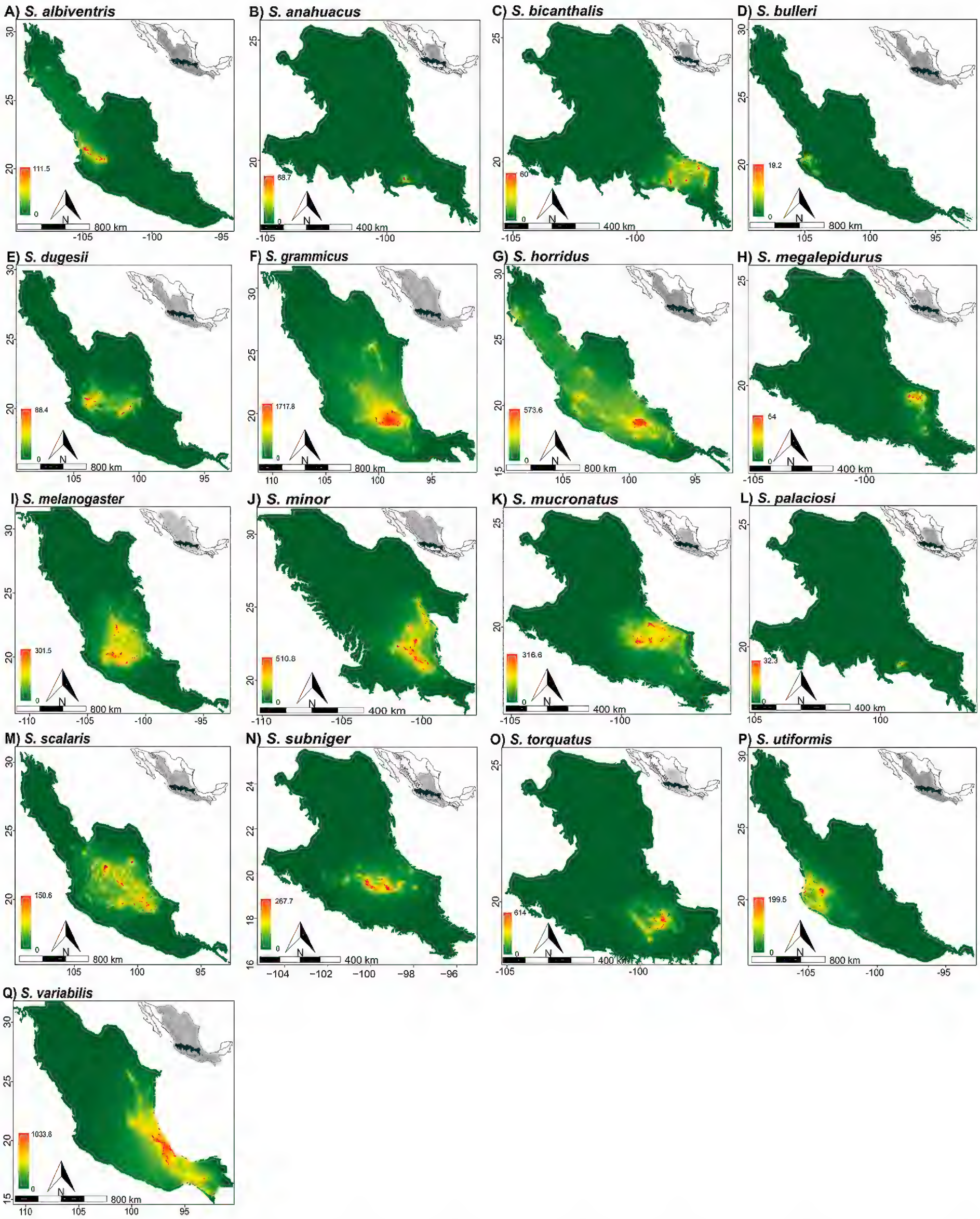

Figure 4. Landscape connectivity maps of 17 species of the genus *Sceloporus*. The gradient in the upper right corner indicates the degree of connectivity of each species in its study area. In the upper right corner, a map of Mexico (in grey) shows the study area M for each species, with the Trans-Mexican Volcanic Belt (TMVB) highlighted in green.

S. bicanthalis, which may be at risk if current anthropogenic pressures persist or intensify. Conversely, species such as *S. variabilis*, *S. scalaris*, *S. mucronatus* and *S. melanogaster* had notably negative index values, indicating broader, more

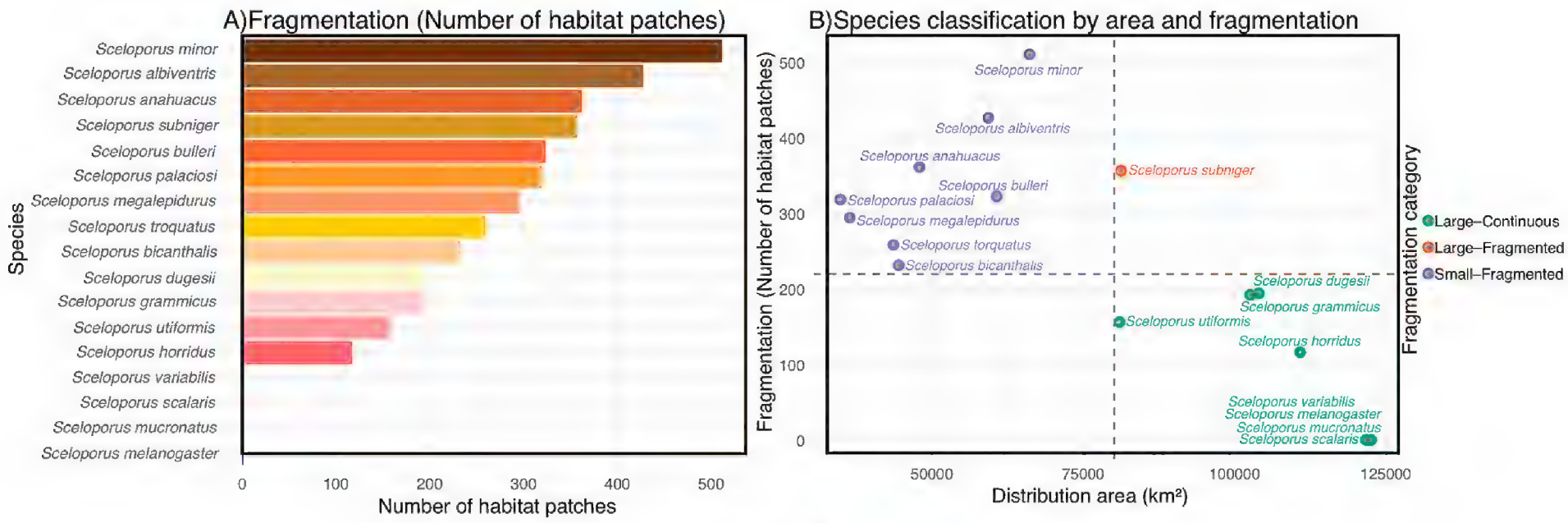

Figure 5. Habitat fragmentation metrics by species. **A.** Number of habitat patches per species; **B.** Mean patch size (km²) across species; **C.** Composite vulnerability index based on normalised values of habitat area, patch number and patch size. The bars represent relative spatial vulnerability; red tones indicate higher risk due to fragmentation and isolation.

continuous and less fragmented potential distributions. Our results highlight key differences in spatial vulnerability amongst endemic species in the TMVB and underscore the necessity for species-specific conservation strategies.

Anthropogenic pressure indices by species

Fig. 6A displays the total anthropogenic pressure indices (%) for each of the 17 analysed *Sceloporus* species in the Trans-Mexican Volcanic Belt (TMVB). Notably, *Sceloporus megalepidurus* and *S. bicanthalis* exhibited the highest levels of exposure (> 17%) to potential habitats overlapping with anthropogenic land uses (urban areas, cultivated pastures and agriculture). These species are closely related to the pressure indices of *S. melanogaster*, *S. mucronatus* and *S. scalaris* (~ 15%). In contrast, *S. palaciosi*, *S. bulleri* and *S. minor* exhibited the lowest levels of anthropogenic pressure, with values less than 10%, suggesting that their suitable habitats are currently less impacted by land conversion.

Human-driven threats undermine species conservation through habitat degradation, fragmentation and loss of ecological connectivity – pressures that are magnified when ranges are small or when representation in protected areas is low (Bolom-Huet et al. 2022). Partitioning each species' suitable habitat (threshold ≥ 80/100) into four land-use pressure classes revealed a consistent pattern: urban areas dominated the habitat composition for nearly

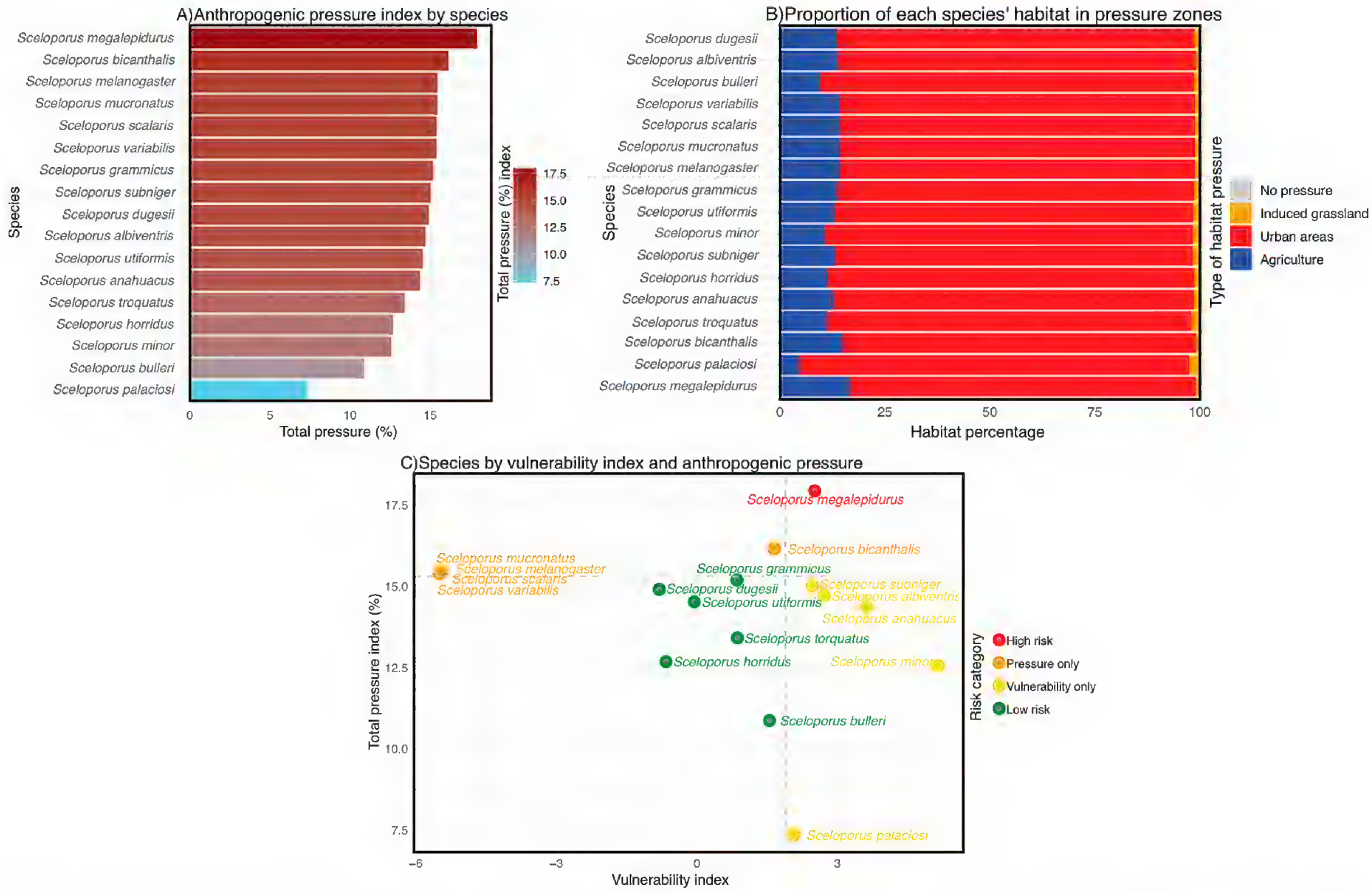

Figure 6. Anthropogenic pressure and vulnerability patterns across species. **A.** Total anthropogenic pressure index (%) for each species, derived from overlap with urban, agricultural and pasture layers; **B.** Proportional habitat exposure to four land-use pressure zones: agricultural (blue), urban (red), induced grassland (orange) and unpressured habitat (grey); **C.** Bivariate plot of vulnerability vs. total anthropogenic pressure. Species are colour-coded by risk category: red = high risk, orange = pressure only, yellow = vulnerability only and green = low risk.

all *Sceloporus* species (Fig. 6B). For several species – *S. megalepidurus*, *S. palaciosi*, *S. bicanthalis* and *S. anahuacus* – more than 80% of the predicted suitable habitat overlapped with urban landscapes, indicating extremely high exposure to human modification; agricultural land generally comprised a smaller fraction and induced pastures contributed only marginally (Fig. 6B). For *S. megalepidurus*, *S. palaciosi*, *S. bicanthalis* and *S. anahuacus*, more than 80% of their habitat is located in urbanised areas, indicating extremely high exposure to human-modified landscapes (Fig. 6B). In contrast, agriculture (blue) contributed a smaller proportion of the total pressure, typically representing less than 20% of each species' habitat (Fig. 6B). Only a few species, such as *S. minor*, *S. horridus* and *S. dugesii*, exhibit modest levels of agricultural overlap.

Induced grasslands (Fig. 6, orange), which often emerge from land degradation or pasture conversion, occupy a small proportion of the habitat, primarily affecting *S. palaciosi*, *S. megalepidurus* and *S. anahuacus*. The absence of natural areas (Fig. 6, grey bars) for nearly all the species indicates that virtually the entire suitable habitat of these lizards is subjected to different levels of anthropogenic pressure (Fig. 6B). This aligns with earlier findings of high fragmentation and low protection coverage, supporting the urgency for conservation actions. The bivariate plot combines the vulnerability index and the total index of anthropogenic pressure. Fig. 6C shows specific conservation profiles amongst the 17 *Sceloporus* species analysed. *Sceloporus megalepidurus* is a "high risk" species because it is the only

species that occupies the upper-right quadrant, as indicated by high values for both vulnerability and pressure. Ten species – including *S. mucronatus*, *S. melanogaster*, *S. scalaris* and *S. variabilis* – are "pressure only" species because they are highly exposed to anthropogenic threats despite lower spatial vulnerability scores. In contrast, the lizards, *S. minor* and *S. palaciosi*, are "vulnerability only" species, characterised by fragmented or limited distributions with minimal overlap with human-modified landscapes. The remaining species, such as *S. bulleri*, *S. torquatus* and *S. horridus*, clustered in the lower-left quadrant, indicating low overall risk due to both low vulnerability and low exposure to anthropogenic pressures (Fig. 6C).

Multivariate anthropogenic pressure analysis and pressure zonation (K-means classification)

The analysis identified four distinct anthropogenic pressure zones across the Trans-Mexican Volcanic Belt (TMVB) (Fig. 7): Zone 1 (green) – Predominantly natural or semi-natural landscapes, including forests and high-elevation areas. These regions exhibit low anthropogenic pressure, but are sparsely distributed and highly fragmented, underscoring the limited extent of pristine habitats within the TMVB. Zone 2 (yellow) – Moderately pressured landscapes characterised by low-intensity land use, such as dispersed agriculture or pasture. These areas function as transitional buffers around urban zones and regions of intensive agriculture. Zone 3 (orange) – Mixed-use landscapes dominated by agricultural activity interspersed with urban development. This zone covers the majority of the TMVB, forming the primary habitat matrix in which most species must persist and disperse, highlighting the prevalence of human-modified environments in central Mexico. Zone 4 (white) – Areas of very high anthropogenic pressure, primarily urban and industrial zones concentrated around major metropolitan centers such as Mexico City, Toluca, Puebla and Guadalajara. These highly transformed environments offer minimal habitat suitability for native biodiversity. This zonation provides a spatial framework for assessing the cumulative impacts of land-use change (LUC) and identifying regions where conservation and restoration interventions are most urgent. The weighted vulnerability richness analysis revealed clear spatial patterns of conservation priority. The vulnerability hotspot map, generated by integrating binary species distributions (threshold ≥ 80) weighted by species-specific vulnerability indices, highlighted several high-priority regions. Hotspots – represented by brighter yellow and orange tones – were concentrated in the eastern TMVB (Puebla and Veracruz highlands), the Sierra de las Cruces between Mexico City and Toluca and montane areas of western Jalisco and Nayarit. Conversely, darker areas corresponded to regions with low species richness or a predominance of species with low vulnerability indices. This mapping approach offers powerful visualisation of conservation urgency, enabling the identification of priority areas where protection or restoration actions could simultaneously benefit multiple at-risk species.

Temporal trend of forests cover loss (2001–2023)

To assess deforestation patterns within the Trans-Mexican Volcanic Belt (TMVB), we analysed annual forest cover loss from 2001 to 2023 using data extracted from the Global Forest Watch platform (Fig. 8A). The dataset revealed

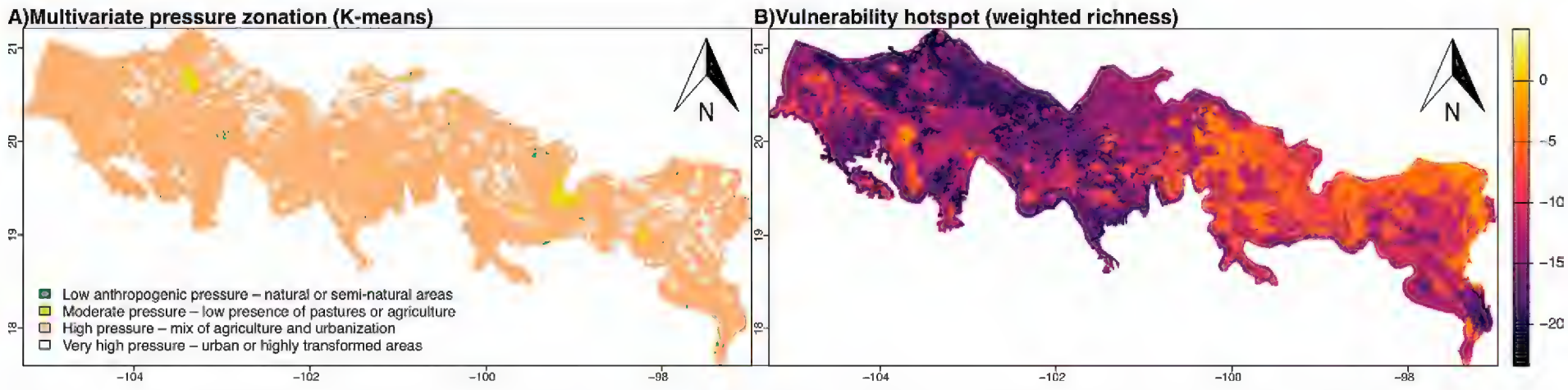

Figure 7. A. Multivariate pressure zonation across the TMVB. K-means clustering (k = 4) of PCA-derived axes from binary urban, agricultural and pasture layers. Green: low anthropogenic pressure (natural/semi-natural). Yellow: moderate pressure (low-density agriculture/pasture). Orange: high pressure (mixed agriculture-urban). White: very high pressure (urban/industrial). This zonation highlights the spatial structure of cumulative human impact; **B.** Vulnerability hotspot map (weighted richness). Spatial distribution of weighted species richness across the TMVB, with brighter areas indicating greater concentrations of vulnerable species. Vulnerability was weighted by each species' composite index. Darker zones represent either low richness or species with low vulnerability scores.

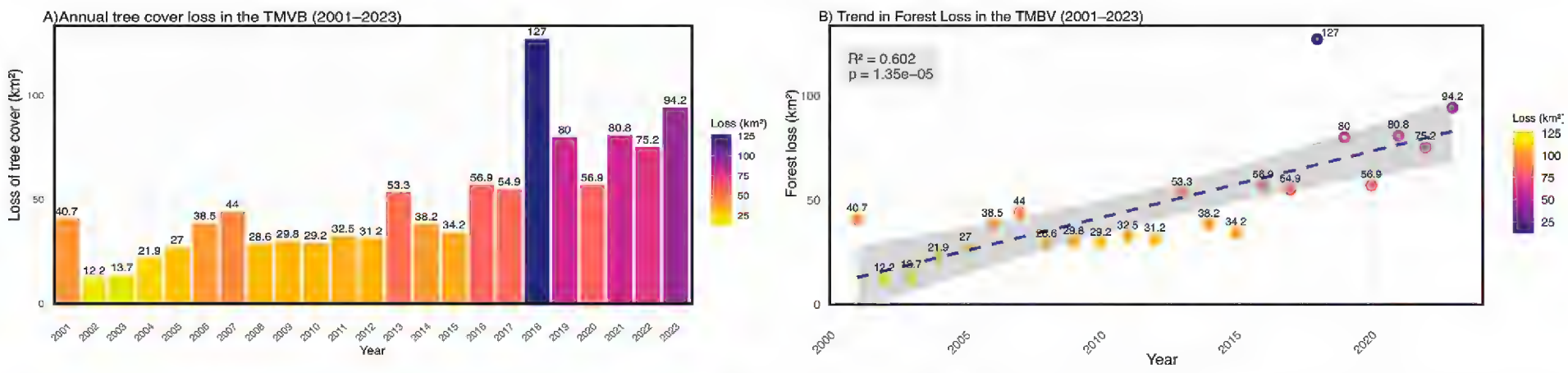

Figure 8. Temporal trend in forest loss across the TMVB (2001–2023). **A.** Annual forest loss (km^2) from Global Forest Watch. The values indicate areas with > 30% canopy loss for trees > 5 m in length; **B.** Linear regression showing a statistically significant positive trend ($R^2 = 0.602$, $p = 1.35 \times 10^{-5}$), indicating increasing deforestation over time. Point colours reflect loss intensity according to the viridis scale.

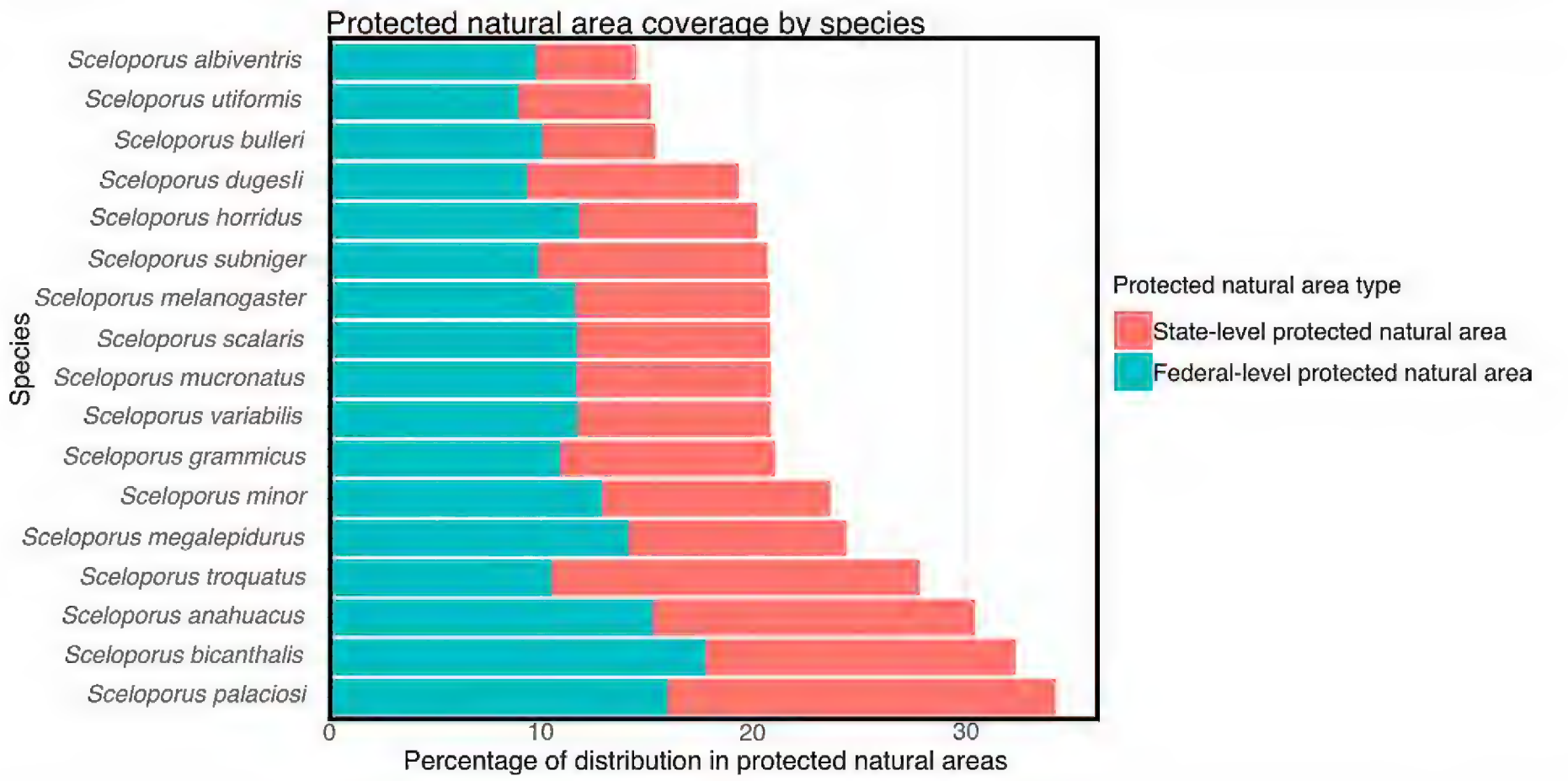

Figure 9. Overlap between species distributions and protected natural areas. Bar chart showing the percentage of each species' range that overlaps with federal (blue) and state-level (red) protected areas. The results highlight discrepancies in protection coverage amongst species, most of which rely heavily on state-level reserves.

fluctuations in tree cover loss across years, ranging from 12.2 km^2 in 2002 to a peak of 127.0 km^2 in 2018, with additional high-loss years observed in 2023 (94.2 km^2) and 2019 (80.0 km^2). The cumulative forest loss over the period was approximately 1242.0 km^2 (Fig. 8A). These values correspond to areas with > 30% canopy loss for trees taller than 5 m and represent deforestation events potentially affecting *Sceloporus* habitats. A linear regression model was used to evaluate the temporal trend in forest cover loss (Fig. 8B). The results showed a statistically significant positive trend ($R^2 = 0.602$, $p = 1.35 \times 10^{-5}$), indicating that forest loss increased considerably over time across the TMVB (Fig. 8B). These findings suggest that anthropogenic drivers of deforestation, such as urban expansion, agriculture, and fire, may be intensifying in this region. The trend was visualised with a scatter plot and a dashed regression line with 95% confidence intervals. Forest loss values were coloured using a viridis palette to enhance contrast between low- and high-loss years and each value was labelled directly on the graph. The pronounced upward trajectory reinforces the urgency of integrating deforestation dynamics into biodiversity vulnerability assessments and regional conservation strategies.

Overlap with protected natural areas

The species *Sceloporus palaciosi*, *S. bicanthalis* and *S. anahuacus* had the highest total protection, with up to ~ 33% of their distributions falling into protected natural areas and splitting between federal and state jurisdictions (Fig. 9). On the other hand, the species at the top of the graph (e.g. *S. albiventris* and *S. utiformis*) exhibited less than 20% protection (Fig. 9). In addition, the majority of their coverage is related to State-level protected areas, suggesting weak federal representation. A few species (e.g. *S. melanogaster*, *S. scalaris* and *S. mucronatus*) exhibited relatively balanced contributions from both protection types. Federal protection alone is rarely sufficient; most species rely on a combination of federal and state-level coverage to reach even minimal representation (Fig. 9).

Discussion

Understanding the environmental constraints and anthropogenic threats related to the distribution of reptile species is essential for developing conservation strategies. They must reflect the current and future pressures acting against biodiversity. In the case of the genus *Sceloporus*, a highly diverse and predominantly endemic group from Mexico, evaluating vulnerability beyond geographic range size has become increasingly important. Our study advances this goal by integrating multiple spatially explicit analyses considering habitat conditions and the intensity of human-induced landscape changes. A major strength of our research lies in the incorporation of land-use variables into the ecological niche modelling framework. While climatic variables (including temperature, precipitation and solar incidence) exhibited substantial contributions across most species, we also observed the significance of land-cover types in certain cases.

Our findings align with those of Urbina-Cardona et al. (2006), who suggested a deep association between amphibian and reptile species and environmental factors such as vegetation cover, temperature and relative humidity, which indirectly influence factors, such as food and shelter availability. From the

models derived, two overarching distribution patterns within this species group can be delineated. *Abies*, species exhibiting broad potential distributions; positively correlated with urban areas (e.g. *S. albiventris*, *S. dugesii*, S. *grammicus*, *S. horridus*, *S. mucronatus* and *S. variabilis*); or with climatic variables (e.g. *S. bulleri*, *S. melanogaster*, *S. minor*, *S. scalaris* and *S. utiformis*), which extend across highland regions and the Eastern or Western Sierras. Conversely, species with more restricted distributions, primarily confined to the elevated areas of the TMVB (e.g. *S. subniger*, *S. anahuacus*, *S. bicanthalis*, *S. megalepidurus*, *S. palaciosi* and *S. torquatus*), are often associated with native vegetation, particularly *Pinus* and *Abies* forests. The negative relationship between the percentage of arid vegetation and the distributions of several species can be explained by their reliance on solar radiation to reach basal body temperatures. However, excessive exposure to high temperatures poses the risk of overheating and mortality, underscoring the importance of thermal shelters (Huey and Stevenson 1979; Sinervo et al. 2010). Notably, species with broader distribution ranges have demonstrated greater capacities for thermal acclimatisation than do those with more restricted ranges. This adaptive flexibility potentially enhances the ability of these Spiny Lizards to colonise new habitats and renders them less vulnerable to the adverse impacts of climate warming (Deutsch et al. 2008; Sunday et al. 2011; Markle and Kozak 2018).

The preference for urban areas amongst certain species may be attributed to their adaptability to these environments, where they can find thermal shelters and other environmental amenities, albeit at the expense of associated drawbacks. Notably, the areas exhibiting the highest habitat suitability and connectivity values for several target species are situated within the mountainous regions of the TMVB, nested amidst sprawling metropolitan cities, such as Mexico City, the Toluca Valley and Puebla (See Suppl. material 1: fig. S2). The forested expanses of this region hold significant commercial value owing to their timber resources (FAO 2010; Pérez-Miranda et al. 2011) and the availability of water resources (Del Campo et al. 2019). Consequently, substantial deforestation events and land-use changes related to agricultural expansion and infrastructure development have been observed in recent decades (Velázquez et al. 2002; Rosete-Vergés et al. 2014; Monjardín-Armenta et al. 2017; CONAFOR 2020; De Alba Rosano et al. 2020), with indications that this trend will persist.

The TMVB is a significant biodiversity hotspot in the country (Mastretta Yanes et al. 2015; González-Fernández et al. 2018; Sunny et al. 2022; Rubio-Blanco et al. 2024). In this study, three pivotal sites for lizard distribution and connectivity were pinpointed. The pivotal sites are important for other endemic reptile species in the country (Sunny et al. 2023). The three sites included "Sierra de las Cruces", which delineates the Toluca and Mexico City valleys and emerged as the primary connectivity hub for the seven species in our study. Despite the presence of federally protected natural areas such as "Desierto de los Leones" and "La Marquesa National Park", along with State-level protected areas, such as "Otomí-Mexica Park", these areas are experiencing significant degradation. Issues such as the expansion of upscale residential areas and associated infrastructure, similar to the "Toluca-Naucalpan highway", are grave concerns (Mejía 2012). Strengthening connectivity between the "Nevado de Toluca", the "Sierra de las Cruces" and the "Chichinautzin Biological Corridor" in the southern Toluca Valley region is deemed essential, given the moderate to

low connectivity levels indicated by our models. The valley area of Jalisco, bordering the State of Nayarit (See Suppl. material 1: fig. S3), emerged as the primary region for seven species, despite the presence of protected areas such as the "La Primavera" and "Sierra de Quilla" APFFs. In Nayarit, the Municipalities of Tepic, Santa María del Oro, Jala and Ixtlán del Río stand out due to their rugged relief, providing relevance for at least three species. Notably, a low-altitude relief pass was identified between "Sierra del Pinabete" and "Sierra Madre del Sur" in the Municipality of Ixtlán del Río, connecting it with the aforementioned area of Jalisco (INEGI 2005). Hence, this region is suggested to constitute a potential corridor for species connectivity in the western region. A comparison of our results with those of a previous study utilising the same algorithm (ENMeval) and environmental variables (Vargas-Jaimes et al. 2021) revealed that the calculated potential distribution areas for *S. anahuacus*, *S. bicanthalis*, *S. megalepidurus* and *S. palaciosi* were smaller than the area calculated for the endemic salamander *Pseodoeurycea leprosa* (34,824 km^2). Despite being classified as "least concern" (LC) on the IUCN Red List and "Threatened" (A) according to NOM-059 and SEMARNAT (2002), due to its high association with forest cover variables and low temperatures, this salamander has a greater conservation status than these Spiny Lizards, suggesting a need for risk re-categorisation.

The potential distributions of *S. subniger* and *S. anahuacus* are largely influenced by the presence of *Abies* forests, which are predominantly found in the mountainous regions of the TMVB and are increasingly threatened by encroaching on legal and illegal logging (González-Fernández et al. 2022). With rising global temperatures, shifts in species altitudinal ranges are anticipated (Bonino et al. 2014; Sillero 2021). Evidence of such shifts has already been observed in *S. megalepidurus* (Díaz de la Vega-Pérez et al. 2022) and *S. utiformis* (Muñoz-Nolasco et al. 2022), attributed to climate change-induced habitat alterations. Oviparous species of the genus *Sceloporus* are reportedly more vulnerable to global warming than sympatric viviparous species (Ma et al. 2022). However, Chiu-Valderrama et al. (2022) documented a contraction in the distribution range of *S. grammicus* (a viviparous species) under climate change scenarios. To mitigate the effects of isolation and limited connectivity, we propose the implementation of local management strategies. These strategies involve enriching the environment by increasing thermal and ecological refuges in areas devoid of vegetation, such as isolated trees located at the intersection of forest fragments, conserving secondary vegetation along forest edges and establishing "living fences" (Urbina-Cardona et al. 2006). Additionally, measures should be taken to avoid the extraction of stones, which serve as important shelter and basking sites. There is also an urgent need to address deforestation practices and prevent the invasion of exotic domestic species in natural environments (Sunny et al. 2024b). For species associated with anthropogenic environments, strategies should focus on fostering a harmonious reptile–human relationship and dispelling misconceptions and aversive beliefs regarding this group of organisms. A key objective of our study was to compare Maxent models optimised with ENMeval with ensemble models optimised with biomod2.

Various studies have demonstrated that models with different levels of complexity can yield significantly different predictions of suitable areas for species (Elith et al. 2010; Anderson and González 2011; Shcheglovitova and

Anderson 2013). Although the evaluation values of the models produced by both algorithms indicated high reliability in terms of the predictions, the Ensemble models proposed broader distribution ranges than those generated by ENMeval for more than half of the species, as indicated by the calculated area. To increase the accuracy of ecological niche estimations for these and other species, it is essential to incorporate variables that capture interactions within the biotic space, such as those representing co-habiting species in the geographical area (Araújo and Luoto 2007). Furthermore, variables indicating human impact should be included in estimating suitability gradients and tolerance to disturbance (Ochoa-Ochoa and Ríos-Muñoz 2019). The potential distribution models proposed in this study represent valuable tools for conservation efforts and decision-making processes. Regarding the ecological niche modelling, we observed a significant contribution of climatic variables, particularly maximum temperature and solar radiation level, which aligns with expectations given the ectothermic nature of these organisms (Rivera-Rea et al. 2023; Plasman et al. 2025). However, certain land-cover variables, notably *Pinus* forests, *Abies* forests and urban areas, also exhibited notable contributions to the presence of several species. TMVB has emerged as a critical area for the distribution and conservation of Spiny Lizards, with projections indicating high habitat suitability and connectivity for most species within this region. Within the TMVB, we identified three sites characterised by these favourable conditions, with the Sierra de las Cruces standing out as particularly crucial for the conservation and maintenance of connectivity amongst several species studied here, as well as other endemic species in the area. Additionally, we recommend revisiting the risk categorisation of certain species, such as *S. anahuacus*, *S. bicanthalis*, *S. megalepidurus* and *S. palaciosi*. The spatial prioritisation analysis integrating vulnerability and exposure to anthropogenic pressures revealed that five species – *S. anahuacus*, *S. albiventris*, *S. bicanthalis*, *S. megalepidurus* and *S. minor* – exhibited both high habitat fragmentation and low protection coverage, classifying them as high priorities for conservation.

Our analysis of habitat composition across multivariate pressure zones revealed an alarming pattern: the vast majority of suitable habitats for *Sceloporus* species are embedded within anthropogenically modified landscapes, particularly urban areas. Urban zones account for more than 80% of the predicted habitats of several species, including *S. megalepidurus*, *S. palaciosi* and *S. bicanthalis*, all of which are endemic to highland regions of the TMVB. These results suggest a substantial mismatch between current land-use dynamics and the ecological requirements of these lizards. The nearly complete absence of habitat in “no pressure” zones for most species underscores a critical conservation concern: even species currently classified as “least concern” (e.g. *S. anahuacus* and *S. grammicus*) may face hidden risks due to high exposure to urbanisation and habitat transformation. The composite vulnerability index also provided key insights. Species with the highest vulnerability scores, *S. minor*, *S. anahuacus*, *S. albiventris* and *S. megalepidurus*, were characterised by highly fragmented and reduced habitat patches, posing threats to meta-population dynamics and long-term viability. Conversely, species such as *A*, *S. scalaris* and *S. mucronatus* had low vulnerability scores, likely reflecting broader, more continuous habitats that buffer them against anthropogenic disturbance. Bivariate

analysis combining the composite vulnerability index and the total anthropogenic pressure index revealed that only *S. megalepidurus* fell within the "high-risk" quadrant. Two species, *S. anahuacus* and *S. bicanthalis*, were classified as "pressure only," while species such as *S. minor* and *S. palaciosi* were classified as "vulnerability only". Species such as *S. bulleri* and *S. horridus* were categorised as "low risk". These results suggest that conservation risk may be underestimated for some species solely based on IUCN designations. Trends in forest loss from 2001 to 2023 revealed a statistically significant increase ($R^2 = 0.602$, $p = 1.35 \times 10^{-5}$), corroborating the findings of previous studies indicating the region's ongoing deforestation and land-use change (López-García and Navarro-Cerrillo 2021; González-Fernández et al. 2022; Ruiz-Reyes et al. 2024; Segarra et al. 2024). This trend aligns with the overlap between the distributions of high-vulnerability species and deforested zones. High fragmentation values in species, such as *S. megalepidurus* and *S. bicanthalis*, highlight the compounded risks of small and isolated populations, which could generate inbreeding problems (Sunny et al. 2019, 2022).

The spatial overlap between species distributions and protected natural areas indicated that several vulnerable species have limited coverage under current conservation schemes (Kearney et al. 2022). This is particularly true for species, such as *S. minor* and *S. megalepidurus*, where federal-level protection is minimal. These findings underscore the need to re-assess the design and location of protected areas and to strengthen legal protection in zones of rapid land transformation. Moreover, we observed considerable gaps in protected area coverage. The ranges of several species were largely excluded from both federal and state-level protected natural areas, emphasising the need to re-evaluate current conservation policies (Ma et al. 2025). This was particularly true for species located in transitional zones between urban and natural habitats, where conservation enforcement is typically weaker. The bivariate classification framework we used – combining vulnerability and protection status – offered a practical method to prioritise species. Notably, species considered as "Least Concern" by the IUCN (e.g. *S. anahuacus*, *S. bicanthalis* and *S. palaciosi*) were flagged in our assessment as high risk, illustrating the limitations of current status designations, based solely on geographic range or known population trends. Our approach thus supports the inclusion of more spatially explicit and ecologically integrative metrics in conservation risk assessments (Zurell 2022).

In conclusion, the combination of ecological niche modelling, landscape connectivity, habitat fragmentation metrics, land-use pressure analysis, and protected area overlap enabled a more comprehensive vulnerability assessment. This multifaceted framework allowed us to identify overlooked risks and conservation gaps amongst TMVB-endemic *Sceloporus* species. Future conservation efforts should integrate forest loss monitoring and habitat connectivity strategies, particularly in zones of rapid land transformation, to mitigate biodiversity decline in this globally significant biogeographic region.

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Additional information

Conflict of interest

Financial support was provided by the Autonomous University of Mexico State. Armando Sunny reports a relationship with the Autonomous University of Mexico State that includes employment. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Ethical statement

No ethical statement was reported.

Use of AI

No use of AI was reported.

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Author contributions

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Data availability

The data will be made available upon request.

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Supplementary material 1

Supporting information of assessment of the vulnerability of Spiny Lizards

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Data type: docx

Explanation note: Supporting information of Assessment of the vulnerability of Spiny Lizards in Central Mexico under anthropogenic pressure: integrating habitat suitability, landscape connectivity, fragmentation, and protected area coverage.

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